Chapter 9

Experimental evidence for the influence of food availability on incubation attendance and hatching asynchrony in the Australian reed warbler

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ABSTRACT

The amount of time a bird allocates to incubation is likely to be limited by energetic constraints. If food is abundant, energetic constraints may be reduced and the time spent incubating (incubation attendance) may increase. Moreover, the onset of incubation in relation to clutch completion may be advanced, resulting in a higher degree of hatching asynchrony. We measured the effect of experimentally increased food availability on incubation attendance and an estimate of hatching asynchrony in the Australian reed warbler (*Acrocephalus australis*). Supplementary food was provided every other day, from a few days before the start of egg laying until just prior to hatching. Incubation attendance was measured with temperature loggers at nests receiving supplementary food and control nests . Hatching asynchrony was inferred from mass and size differences between siblings shortly after hatching. We found that 1) food supplementation resulted in an increase in incubation attendance, when comparing both nests receiving supplementary food to control nests as well as feeding to non-feeding days in nests receiving supplementary food, and 2) food supplementation resulted in a greater hatching asynchrony, without affecting clutch size, average egg volume or the likelihood of eggs hatching. This suggests that food availability acts in a proximate way to modify the extent of incubation attendance and hatching asynchrony. We discuss the adaptive significance of increased incubation attendance and a shift in the degree of hatching asynchrony in relation to food availability.

INTRODUCTION

The importance of the level of incubation attendance (i.e. the proportion of time a bird spends incubating) for parental fitness has been underestimated in studies on avian breeding biology compared to physical factors such as clutch size and egg volume (Hébert 2002). Since incubation is an energetically costly activity, the level of incubation attendance should be connected to either proximate or ultimate energetic constraints (Slagsvold 1986; Slagsvold & Lifjeld 1989). The greater the energetic demand, the greater the need for the incubating bird to forage (MacCluskie & Sedinger 1999; Ellis *et al.* 2001). The amount of food available to an incubating bird is therefore expected to have a direct effect on the trade-off between foraging and incubation (Moreno 1989; MacCluskie & Sedinger 1999), and this effect should be particularly strong in species in which only the female incubates and which lack male incubation feeding (Lyon & Montgomerie 1985; Nilsson & Smith 1988). Consequently, an increase in food availability may result in an increase in incubation attendance (Drent *et al.* 1985; Rauter & Reyer 1997).

Energetic constraints on incubation may be particularly strong during the period of egg production and may affect the onset of incubation in many species. Thus, birds which are less constrained by the need to forage may start incubating before clutch completion, thereby generating a higher degree of hatching asynchrony ('energetic constraints hypothesis'; Slagsvold 1986). Asynchronous hatching of a clutch has been shown to have an effect on parental fitness in many species (see Krebs 1999 for a review). Whether asynchronous hatching increases (e.g. through 'time saving' benefits, see Discussion) or decreases (e.g. through higher mortality of last hatched nestlings) fitness will depend, among other factors, on the prevailing food circumstances while raising the young (Hillstrom *et al.* 2000; Royle 2000).

During periods of abnormally cold weather, hatching asynchrony is lower (Enemar & Arheimer 1989; Slagsvold & Lifjeld 1989). During such periods, incubation will be more strongly constrained because the incubating bird's energy requirements, and thus the need to forage, will be high and foraging efficiency might be reduced (Neal *et al.* 1993; Pasinelli 2001). These studies suggest that incubation behaviour is constrained by food availability both before and after clutch completion.

If high food availability alleviates the costs of incubation, then incubation attendance and the extent of hatching asynchrony resulting from an advanced onset of incubation should increase, irrespective of the benefits (Nilsson 1993). There is very little evidence for an effect of food availability on incubation attendance, and only one study has shown that the broods of females which received extra food during egg-laying had greater hatching asynchrony than control broods (marsh tits *Parus palustris*; Nilsson 1993). Furthermore, no previous study has addressed the effect of food availability on both incubation attendance and hatching asynchrony simultaneously. The aim of this study was to measure the effect of experimentally increased food availability on incubation attendance and an estimate of hatching asynchrony in the Australian reed warbler *Acrocephalus australis*. The Australian reed warbler forages mainly on aerial insects (Barker & Vestjens 1990) and has several clutches per season. Males vigorously defend small territories around the nest

against conspecifics. Only the female incubates (Welbergen *et al.* 2001) and male incubation feeding is negligible (occurred only twice in approximately 30 h of incubation observations). These features make it a good species to study the effect of food supplementation on incubation attendance and hatching asynchrony. We predicted that an increase in food availability would result in both an increase in incubation attendance and a higher estimate of hatching asynchrony.

METHODS

Supplementary feeding

This study was conducted during two breeding seasons (September to January) in 1999/2000 and 2000/2001 in a 10 ha. plot of Australian reed (*Phragmites australis*) surrounding a lake near Melbourne, Australia (38º 02'S, 145º 07'E). The supplementary feeding experiment was carried out throughout both breeding seasons. Twenty-nine (12 in 1999/2000; 17 in 2000/2001) experimental and 97 (46 in 1999/2000; 51 in 2000/2001) control nests were randomly assigned, but the number of experimental nests was limited by the amount of supplementary feeding that could be performed. Control nests were treated in exactly the same way as experimental nests, except for the presence of supplementary food trays. In the breeding territories of experimental nests, escape-proof plastic trays (20 cm diameter, 3 cm deep) were placed approximately 2 meters from the nest and were filled with 30 g of live blowfly maggots (in processed bran or rice husks) every other morning at approximately 11.00 h AEST. The alternation of a feeding and non-feeding day provides the opportunity for an intra-nest comparison. The energy content of these maggots is approximately 4.5 kJ/g (Inaoka *et al.* 1999). For an incubating female Australian reed warbler with an estimated field metabolic rate of 80 kJ per day (Williams 1996), 30 grams of maggots represent over 1.5 times her daily energy requirements. Supplementary feeding in each territory was stopped prior to the hatching of the first egg in that territory and therefore was very unlikely to have an effect on early nestling growth. The supplementary feeding always started shortly (2.5 days ± 1.7 SD) before the beginning of egg laying, therefore the potential effect on female body condition during egg laying would be minimal (Wiggins 1990; Erikstad *et al.* 1993; Pietiäinen & Kolunen 1993). Most individuals were caught in mist nests and colour banded with a unique colour combination for individual recognition. Remote video observations (2.75 h ± 0.9 SD each, $n = 7$) of colour-ringed birds revealed that both male and female reed warblers routinely consumed the majority of the supplementary food and that no other bird species fed on the maggots. Supplementary food was almost always completely gone by the following morning. Excess food was not removed, and practical considerations precluded us from providing maggots on an *ad libitum* basis.

Incubation attendance

Temperature logger (TL; Gemini Data Loggers Ltd., Chichester, U.K.) measurements were gathered in November 2000 only. On a random day during incubation, after clutch com-

pletion, small temperature probes were inserted into the nest-cups of both experimental (randomly with respect to supplementary feeding and non-feeding days) and control birds, to a level just below the top of the eggs. The TL recorded the temperature in the nest every 60 seconds for a continuous period of either 36 or 72 hours, depending on the type of logger. In a TL temperature graph, a large and sudden increase in temperature corresponded with the start of an incubation bout and a large and sudden drop with the end of the incubation bout. Three nests were filmed for 3-4 h at the beginning of the TL recording period in order to validate the analyses of the temperature graphs and measurements of incubation attendance were very similar for TL and video analyses (only 3.4 % time difference). A comparison of incubation attendance between experimental and control nests was made over the final 24-h of the TL recording period. In experimental nests, an intra-nest comparison of incubation attendance was also made between a single feeding and a single control day (in random order) from 12.00-18.00 h (this corresponds to the period directly after feeding on feeding days). In addition, incubation attendance was recorded between the laying of the second and third eggs in two experimental nests and one control nest. Weather data were taken from the Moorabin airport weather station, five km from the study site.

Egg and nestling measurements

For all eggs found in the breeding season of 2000/2001, maximum length and width was measured (to the nearest 0.1 mm) using a vernier calliper. Egg volume was calculated using the equation: Volume = 0.507 x length x width^2 (Hoyt 1979). Hatchability of a clutch (i.e. the proportion of the eggs in a clutch that hatched) was calculated for non-predated clutches. In both years, one to three days after hatching, nestling mass (to the nearest 0.1g) and tarsus length (to the nearest 0.1 mm) were measured using a spring-balance (Pesola) and a vernier calliper, respectively.

Hatching asynchrony

The estimate of hatching asynchrony was quantified as the relative difference in mass and tarsus size of nestlings. The relative differences in nestling mass or size were calculated as: [(first-hatched nestling) – (last-hatched nestling)] / (mean of all nestlings) (following Skagen 1988; Bryant & Tatner 1990; Amundsen & Slagsvold 1991; Wiebe & Borlotti 1994; Krebs 1999). In order to exclude a possible effect of competitive interactions between siblings on the estimate of hatching asynchrony, measures of the mass or size hierarchy within a brood were only calculated for broods in which the mass of the heaviest nestling was less than 5 g (corresponding to mass at 3 days; Berg 1998). Although actual hatching time differences within a clutch were not routinely measured in order to minimise disturbance, we did identify eleven additional broods that did not receive supplementary food and were known to hatch with < 1 day asynchrony (by checking these nests for two consecutive days around hatching time). This enabled verification that large relative differences in nestling mass or size did not develop in relatively synchronously hatching broods (see results). Data on chick mass and size have been pooled for the two years (1999/2000: 4 experimental and 7 control nests; 2000/2001: 6 supplementary and 11 control nests).

The relative differences in size of young nestlings may depend on the relative difference in egg volume in a clutch (Perrins 1996). Therefore, a comparison of egg volume differences was made between experimental and control nests by calculating a measure of egg volume asymmetry in a similar way to the hatching asynchrony estimate (2000/2001 only).

Statistical analyses

All statistical tests were performed using SPSS 11.0 for Windows and methods followed Quinn & Keough (2002). Proportional data were arcsin transformed prior to testing which improved normality. We used univariate general linear models (GLM) to test hypotheses about the effect of supplementary food on both incubation attendance and relative size and mass differences of hatchlings (dependent variables). In the GLM examining incubation attendance (dependent variable), we included supplementary feeding treatment as a fixed factor and weather (temperature (°C), precipitation (mm), dew point temperature (°C) and wind speed (km/h)), clutch size, laying date, and age of the clutch (days since clutch completion) as covariates. There was little collinearity between the covariates (all tolerance values ≥ 0.2). All measurements were taken in a single study year.

To examine relative mass and size differences, we used GLMs with the hatching asynchrony estimate as the dependent variable, treatment (supplementary feeding, control) as a fixed factor, and brood size as a covariate. The distribution of year and brood sizes across the two treatments was equal, so these variables were not including in the model. An additional GLM which included brood size was used to compare the experimental and control nests with nests known to have < 1 day hatching asynchrony.

For the intra-nest comparison of incubation attendance, a paired samples *t*-test was used. We compared clutch size, average egg mass of a clutch, mean volume, volume asymmetry and hatchability between experimental and control nests using *t*-tests. The start, duration and end of the nightly incubation bout, daytime incubation bouts, daytime recesses and the frequency of recesses were also compared between experimental and control females using *t*-tests. Power analysis was carried out using the G*Power computer program (Faul & Erdfelder 1992). All *P*-values reported are 2-tailed and considered significant when $\alpha < 0.05$.

RESULTS

Clutch variables

Although it is likely that Australian reed warblers produce eggs primarily using energy and nutrients consumed during the previous day (income breeders; Perrins 1996), supplementary feeding did not have an effect on clutch size, average egg volume or relative egg volume differences within a clutch (Table 9.1). Hatchability did not differ between experimental and control nests (Table 9.1).

Incubation attendance

Incubation attendance was significantly increased by the supplementary feeding treatment

Table 9.1. Hatchability, mean egg volume within a clutch, clutch size and relative egg volume differences (volume hierarchy) in clutches of females receiving supplementary food and control females. Power is the probability that the test will yield statistically significant results ($\alpha = 0.05$).

	Treatment	*n*	Mean ± SD	*t*	*P*	Power
Hatchability (%)	Supplementary fed	12	0.92 ± 0.14	1.01	0.32	0.18
	Control	41	0.86 ± 0.20			
Mean volume (ml)	Supplementary fed	17	2.43 ± 0.12	0.80	0.43	0.11
	Control	51	2.40 ± 0.17			
Clutch size	Supplementary fed	17	2.82 ± 0.39	-0.39	0.70	0.07
	Control	51	2.86 ± 0.35			
Volume asymmetry	Supplementary fed	17	0.25 ± 0.09	0.47	0.64	0.07
	Control	51	0.24 ± 0.08			

Table 9.2. Start time and duration of the nightly incubation bout and daytime incubation bouts, duration of daytime recesses and the frequency of recesses in females receiving supplementary food and control females. Power is the probability that the test will yield statistically significant results ($\alpha = 0.05$).

	Treatment	n	Mean ± SD	t	P	Power
Start of night time incubation bout (time)	Supplementary fed	12	0827 ± 0043h	-0.46	0.66	0.07
	Control	12	0835 ± 0038h			
End of night time incubation bout (time)	Supplementary fed	12	0545 ± 0018h	0.76	0.46	0.14
	Control	12	0537 ± 0022h			
Duration of night time incubation bouts (h)	Supplementary fed	12	9.38 ± 0.81	0.45	0.65	0.07
	Control	12	9.24 ± 0.83			
Duration of daytime incubation bouts (min)	Supplementary fed	12	4.87 ± 1.47	1.54	0.14	0.32
	Control	12	3.98 ± 1.30			
Duration of daytime recesses (min)	Supplementary fed	12	3.69 ± 1.15	-0.36	0.72	0.06
	Control	12	3.85 ± 1.18			
Recess frequency (per hour)	Supplementary fed	12	7.45 ± 1.70	0.94	0.36	0.15
	Control	12	8.15 ± 1.94			

and was negatively affected by dew point temperature (GLM: $F_{2,20} = 11.9$, $P = 0.008$ and $F_{2,20} = 11.3$, $P = 0.004$, respectively), but not by temperature, precipitation, wind speed, clutch size, laying date, or age of the clutch ($P \geq 0.1$). There was no significant difference in the duration of the night time incubation bout between treatments or in the start or end of this bout (Table 9.2), so we present incubation for the day time period only (Fig. 9.1A).

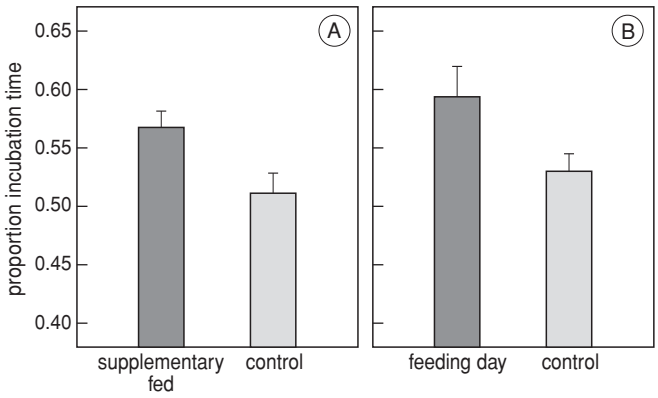

Figure 9.1. (A) Percent incubation time ± SE of females receiving supplementary food (n =12) and control (n = 10) females during the day. (B) Intra-nest comparison of percent incubation time ± SE in nests receiving supplementary food from 12.00-18.00 h (the period directly after feeding on feeding days) on feeding and control days (n =7).

Since dew point temperature significantly affected incubation attendance, we used the residuals of incubation attendance regressed on dew point temperature in the intra-nest comparison of incubation attendance. Females incubated more on a feeding day than on a control day (paired samples t-test: $t_7 = 3.67$, $P = 0.01$; Fig. 9.1B). Of the three nests for which incubation attendance was recorded before clutch completion, all females were already incubating between the laying of the second and third egg. Since there was no significant difference in the start, duration or end of the nightly incubation bout, the higher incubation attendance of experimental females that we observed must be explained by differences in incubation behaviour during the day. While experimental females tended to reduce the recess frequency and duration of daily recesses, and increase the duration of incubation bouts, no significant differences were found between experimental and control females in these variables (Table 9.2), however, the power of these tests was low.

Hatching asynchrony

The hatching asynchrony estimates were higher in experimental nests than in control nests (GLM: $F_{1,28} = 7.06$, $P = 0.013$ for mass, and $F_{1,28} = 6.80$, $P = 0.015$ for size; Fig. 9.2). The hatching asynchrony estimates of broods known to hatch with < 1 day asynchrony were the same as those of control (not supplementary fed) broods (GLM: $F_{2,39} = 5.10$, $P = 0.011$; contrast estimate = 0.02, $P = 0.730$ for mass; contrast estimate = 0.02, $P = 0.471$ for size), but significantly smaller than those of experimental broods (GLM: $F_{2,39} = 4.86$, $P = 0.014$; contrast estimate = 0.17, $P = 0.009$ for mass; contrast estimate = 0.07, $P = 0.007$ for size; Fig. 9.2). This rules out the possibility that the increased hatching asynchrony estimates in the experimental group were established after synchronous hatching. The estimate of hatching asynchrony was higher in larger broods ($F_{2,39} = 6.61$, $P = 0.014$ for mass; $F_{2,39} = 6.92$, $P = 0.013$ for size).

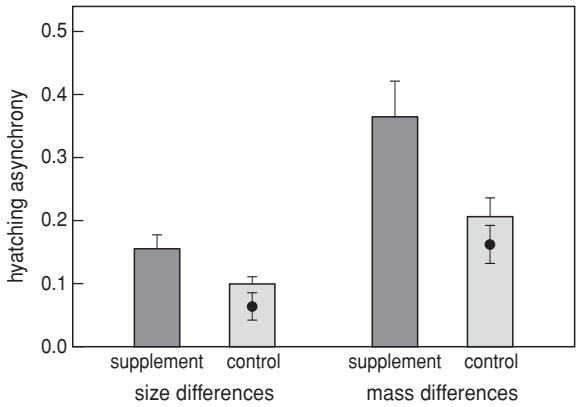

Figure 9.2. Hatching asynchrony estimate ± SE (calculated from size and mass) of hatchlings in broods of females that received supplementary food (n = 10) and control females (n = 19). The closed circles (± SE) represent the hatching asynchrony estimates for broods known to have hatching asynchrony of < 1 day (n = 11).

DISCUSSION

Incubation performance

We found a positive relationship between food availability and incubation attendance in the Australian reed warbler. Notably, this relationship existed not only when comparing experimental and control nests, but also when comparing feeding and non-feeding days in experimental nests. Apparently, incubating female Australian reed warblers are energetically constrained and face a trade-off between incubation and foraging.

Previous studies on wheatears (*Oenanthe oenanthe*; Moreno 1989), blue tits (Parus caeruleus; Nilsson & Smith 1988) and pied flycatchers (*Ficedula hypoleuca*; Sanz 1996) have found that females, which received supplementary food during incubation had a significantly shorter incubation period. If increased incubation attendance caused the clutches of experimental females to hatch sooner (Rodriguez-Teijeiro *et al.* 1997), this should significantly improve their reproductive success, mostly through "time saving benefits". The probability of depredation of the eggs may be lower due to the reduced period of vulnerability (Clark & Wilson 1981; Swennen *et al.* 1993; Persson & Göransson 1999; Conway & Martin 2000a). A shorter incubation period means that the young hatch earlier in the season, which may increase their survival chances (Perrins 1965; Spear & Nur 1994; Dzus & Clark 1998) and enhance their probability of recruitment (Hochachka 1990; Spear & Nur 1994; Verhulst *et al.* 1995; Dzus & Clark 1998).

Dew point temperature negatively affected incubation attendance. A change in dew point may affect the warblers prey availability and consequently their foraging efficiency (Jones 1987), or the water loss of eggs. It remains uncertain which of these factor(s) are responsible for the observed effect of dew point, however, as dew point positively affects male song rate in Australian reed warblers (chapter 5), it is unlikely that a high dew point

increases the birds energetic needs.

Contrary to our findings, several studies have shown that various aspects of incubation behaviour, including nest attendance, duration of incubation bouts and duration of recesses were affected by ambient temperature (e.g. Bryan & Bryant 1999; Reid *et al.* 1999; Conway & Martin 2000a), clutch size (e.g. Arcese & Smith 1988; Wiebe & Martin 2000; Wallander & Andersson 2002), laying date (MacRoberts & MacRoberts 1972; Sockman & Schwabl 2001) and precipitation (Skutch 1962). It is possible that these variables would have affected incubation attendance if they had varied more during the period of measurements. In this study, temperature was measured in open habitat at Moorabin airport, but our population nested in dense reed beds in which fluctuations in temperature may not be as pronounced as at the airport (Kadlec & Knight 1996). Variation in clutch size was very low: 80 % of the nests in which incubation attendance was measured contained three eggs. Measurements of incubation were taken over only a quarter of the entire breeding season (30 days), and precipitation during this period was limited to 4 days.

The energy supplied by the maggots should confer substantial energetic and temporal gains to experimental birds. It is notable then, that the duration of daytime recesses, clutch size, egg volume (Wiebe & Bortolotti 1995; Oro *et al.* 1999) were essentially unchanged in experimental females. We offer four possible explanations for this anomaly. Firstly, females could invest energetic gains from supplementary food into increasing their own survival (Stearns 1992) since for bird species in which only the female incubates, the high energy expenditure during incubation could translate into increased mortality (Williams 1996). Secondly, females may still need to forage for specific nutrients not provided in sufficient quantities by the maggots. Thirdly, the periodic cooling that eggs undergo during recesses may be important to maintain hatching success, particularly in the rather high ambient temperatures most commonly encountered by our population (Kendeigh & Baldwin 1932; Westerskov 1956; Landauer 1967; Batt & Cornwell 1972; Oppenheim & Levin 1975). Finally, Conway & Martin (2000b) argue that species that endure high nest depredation have evolved an incubation strategy that minimizes activity that could attract predators (long incubation bouts and recesses). It is possible that in our study population, predation pressure has constrained the effect of supplementary food on incubation behaviour, especially recess duration.

Hatching asynchrony

The hatching asynchrony estimates (relative mass and size differences between hatchlings ≤ 3 days old) were significantly larger in experimental nests than in control nests. We used an indirect measure of hatching interval and it is possible that the observed size and mass asynchrony may arise after hatching, irrespective of the actual hatching interval. However, we believe that this measure does provide a reliable indication of the actual hatching interval, for several reasons. Firstly, nests known to have relatively short hatching intervals (< 1 day) yielded hatching asynchrony estimates similar to the control group and significantly smaller than the supplementary feeding group, showing that low hatching asynchrony estimates provide reliable indications of short hatching intervals.

Secondly, supplementary feeding was stopped prior to the hatching of the first egg, and remote video observations of food provisioning show that food is equally distributed between the nestlings with respect to size (Berg 1998), so it is unlikely that our hatching asynchrony estimates became disproportionally larger after hatching in experimental nests relative to control nests. Finally, this technique has been used successfully in several previous studies (Bryant & Tatner 1990; Wiebe & Borlotti 1994; Krebs 1999).

Hatching interval may depend on the length of the laying interval, egg volume differences within a clutch, incubation efficiency for each egg and the onset of incubation (Slagsvold 1986). We have no evidence that supplementary feeding affected the laying interval in the Australian reed warbler (M. L. Berg & J. A. Welbergen unpubl. data), although the length of the laying intervals was shortened in the European kestrel (*Falco tinnunculus*; Aparicio 1994) and unaffected in the Nazca boobie (*Sula granti*; Clifford & Anderson 2001) as a result of supplementary feeding. Egg volume asymmetry did not differ between clutches of experimental and control females in the Australian reed warbler. Clutch sizes were relatively small in the Australian reed warbler (2.6 ± 0.7 SD, $n = 213$), so the incubation efficiency is unlikely to be different between eggs, and there was no difference in clutch size between experimental and control nests. It is therefore most likely that the experimental females advanced the onset of incubation. This interpretation is in accordance with the findings of Nilsson (1993), who showed that female marsh tits provided with supplementary food significantly advanced the onset of incubation compared to control females. Apparently not only incubation attendance, but also the onset of incubation is constrained by the energetic requirements of the female reed warblers, which further supports the energetic constraints hypothesis (Slagsvold 1986).

We found that both experimental females ($n = 2$) and one control female incubated during laying, raising the possibility that increased incubation attendance alone of experimental females may have resulted in the sibling mass and size hierarchies that we observed, rather than a change in the onset of incubation. However, the 4% increase in incubation attendance of experimental females compared to control females would amount to no more than 2 h of extra incubation time, assuming equal incubation intensity, which would be insufficient to cause the difference in hatching asynchrony observed between experimental and control nests.

Our finding that the estimate of hatching asynchrony is higher in larger clutches has also been shown in the green-rumped parrotlet (*Forpus passerinus*; Beissinger & Waltman 1991) and in the pied flycatcher (Moreno & Carlson 1989). This may simply be due to the greater age (and growth) advantages of the first hatched nestling in relation to the last hatched nestling in more asynchronously hatching nests.

An earlier onset of incubation may confer similar benefits to those that may arise from a shorter incubation period because a part of the brood hatches earlier. Another benefit of earlier onset of incubation and greater incubation attendance might be better hatchability of the eggs, especially of the first laid egg (Lyon & Montgomerie 1985; Nilsson & Smith 1988; Arnold 1993; Veiga & Viñuela 1993; Viñuela 2000). We did not find an increase in hatchability with increased hatching asynchrony, however, we do not have data on hatchability linked to laying order. In addition, earlier hatched Australian reed warblers may

have a greater ability to escape predators because the chicks of this species readily climb out of their nests and into the reeds in order to escape potential predators prior to fledging (pers. obs., Brown & Brown 1986), and the ability to do so effectively depends largely on their age (pers. obs.). This behaviour also makes it very difficult to accurately determine the true fledging time.

If an earlier onset of incubation has the potential to provide tangible benefits, why is it not a more common strategy? Firstly, the extent to which parents may be able to influence the degree of hatching asynchrony through an earlier onset of incubation will likely be dependent on energetic constraints on incubation (Slagsvold & Lifjeld 1989). These constraints are likely to be particularly important for females during the egg laying period due to the costly energetic and nutrient requirements of egg production (Visser & Lessells 2001), and will be influenced strongly by food availability during this period (Perrins 1996). Secondly, in many species of birds last-hatched nestlings in asynchronous broods have lower growth and survival rates due to their inferior competitive abilities (see Krebs 1999 for a review). If food availability is high during the nestling period, however, the discrepancies in growth and survival between differently aged siblings may be less pronounced (Royle 2000). For these reasons, advancing the onset of incubation may only be a successful strategy during periods of high food availability (Stoleson & Beisinger 1997). By using the food availability during laying as a cue to predict food availability during chick rearing, incubating parents may be able to adaptively manipulate the extent of hatching asynchrony (Royle & Hamer 1998; Wiebe & Bortolotti 1994). As with incubation attendance after clutch completion, this suggests that while other evolutionary forces may favour the outright presence or absence of hatching asynchrony, food availability may act in a proximate way to modify the extent of hatching asynchrony.

In the future, detailed observations on the actual onset of incubation, time of hatching, and measurements of chick growth in relation to food availability are required to fully understand the role of incubation behaviour in hatching asynchrony. Data on survival and recruitment are needed to gain further insights into the adaptive significance of an advanced onset of incubation and increased incubation attendance. Furthermore, this study highlights the need for a greater understanding of the allocation of time and energy by incubating birds in a life-history context.

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